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Molecular characterization of the recombinant inbred line population derived from a *japonica-indica* rice cross

Guangjie Liu · John L. Bernhardt · Melissa H. Jia · Yeshi A. Wamishe · Yulin Jia

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Abstract Recombinant inbred line (RIL) populations of rice are useful genetic sources for map-based cloning of agronomically important genes. Zhe733 is a high-yielding *indica* cultivar from China conferring resistance to rice blast (RB), rice water weevil (RWW) and straighthead; whereas Kaybonnet *low-phytic acid* 1-1 (KBNT*lpa*) is a mutant of a tropical *japonica* cultivar from the US containing low-phytic acid with average yield, and is susceptible to some RB races, RWW, and straighthead. A 355 RIL F_{10-11} population derived from the cross of KBNT*lpa* × Zhe733 was recently released. Simple sequence repeat (SSR) markers were used to evaluate 269 RILs of this population. A total of 107 polymorphic markers were mapped on all rice chromosomes representing a total of 1,016.3 cM of genetic distance. Two hundred and thirty-five KBNT*lpa* × Zhe733 RILs (KZRILs) were clustered into seven groups based on allele frequencies of SSR markers. Twenty-three markers (21.1%) on chromosomes 3, 6, 7, 9, and 11 were found to favor Zhe733 ($\chi^2 = 16.8-189.7$ and $P < 0.01$) and five markers (4.6%) on chromosome 1 and 6 were found to favor KBNT*lpa* ($\chi^2 = 18.5-46.6$ and $P < 0.01$). Marker segregations were observed to be normal for both parents except 26 (10.2%) KZRILs were found to skew toward Zhe733 ($\chi^2 > 15.7$ and $P < 0.01$). Furthermore, the average frequencies of heterozygosity and non-parental alleles per KZRIL were 1.3% (0.0–38.9%) and 0.4% (0.0–15.0%), respectively. Thirteen heterozygous KZRILs were found at more than five markers loci and nine KZRILs were found with more than five non-parental alleles representing 5.1 and 3.5% of 255 KZRILs. Overall, this KZRIL population is a good population with relatively low frequencies of heterozygosity and non-parental alleles, and with relatively low percentages of skewed markers and skewed KZRILs. The profiles of these SSR markers should facilitate molecular tagging critical genes controlling yield, RB, RWW, and straighthead resistance.

Keywords Cluster analysis · Linkage map · Recombinant inbred line · Rice · SSR marker

Abbreviations

KBNT*lpa*	Kaybonnet *low-phytic acid* 1-1
KZRIL	RIL derived from a cross of KBNT*lpa* and Zhe733
RIL	Recombinant inbred line
SSR	Simple sequence repeat

G. Liu · J. L. Bernhardt · Y. A. Wamishe
Rice Research and Extension Center, University of Arkansas, 2900 Hwy 130E, Stuttgart, AR 72160, USA

G. Liu · M. H. Jia · Y. A. Wamishe · Y. Jia (✉)
USDA-ARS Dale Bumpers National Rice Research Center, P.O. Box 1090, Stuttgart, AR 72160, USA
e-mail: yjia@spa.ars.usda.gov

G. Liu
China National Rice Research Institute, 359 Tiyuchang Road, Hangzhou 310006, P.R. China

Introduction

Rice, *Oryza sativa* L., is an important food crop feeding half of the world's population. High yielding rice cultivars with good quality, and improved pest resistance should help to keep pace with increased demand for rice by the rapid expansion of the world population. The defined map positions of agronomically important major genes and quantitative trait loci (QTL) should be useful for the development of improved rice cultivars via marker-assisted breeding.

A recombinant inbred line (RIL) population is commonly used in tagging important rice genes. It is particularly useful for analyzing QTLs since phenotypes can be evaluated over years. For instance, rice RILs have been used in mapping QTLs for submergence tolerance (Nandi et al. 1997), floral morphology (Uga et al. 2003), seedling vigor (Zhang et al. 2005b), blast resistance (Zhuang et al. 2002), sheath blight resistance (Pinson et al. 2005), and cold tolerance (Andaya and Mackill 2003; Zhang et al. 2005a) and in mapping resistance genes to rice planthoppers (Tan et al. 2004).

Commonly used molecular markers for mapping are restricted fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), and simple sequence repeat (SSR). SSR markers are preferred because they are abundant, co-dominant and easily assayed by polymerase chain reaction (PCR) (Cho et al. 1998; Tabien et al. 2000; He et al. 2001) and have been widely used in rice (Ni et al. 2002), maize (Gethi et al. 2002; Heckenberger et al. 2002), wheat (Dreisigacker et al. 2004), and soybean (Boerma et al. 2004). The sequence information and map positions of rice SSR markers are publicly available (http://www.gramene.org) and more rice SSR markers are being developed to tag any possible polymorphic parents (Temnykh et al. 2000; McCouch et al. 2002; International Rice Genome Sequencing Project 2005). More polymorphic markers can be identified and used for mapping if the two parents are more diverse. However, the two most common problems encountered are distorted segregation and high levels of heterozygosity if the two parents are more distally related with one and another. Distorted segregations have been reported in several rice RIL populations (Cho et al. 1998; He et al. 2001). Relatively high levels of heterozygosity have also been documented in several RIL populations of the crosses between *japonica* and *indica* parents (Xiao et al. 1996; Cho et al. 1998).

Kaybonnet *low-phytic acid* 1-1 (KBNT*lpa*) (Rutger et al. 2004) is a mutant of a *japonica* cultivar KBNT with average yield, low-phytic acid (Larson et al. 2000) and is susceptible to straighthead, a physiological disorder of rice that results in sterile florets with distorted lemma and palea (Yan et al. 2005). Recently, it was discovered that KBNT*lpa* is susceptible to new virulent races IE1K and IB-33 of rice blast (RB) (*Magnaporthe oryzae*, formerly *Magnaporthe grisea*) (Lee et al. 2005), one of the most destructive diseases of rice in the world. Zhe733 is a widely grown high-yielding *indica* cultivar from China (Cheng and Min 2000). Zhe733 is resistant to IE1K and IB-33 of *M. oryzae* (Jia et al. 2005; Wang et al. 2007) and to straighthead (Yan et al. 2005). Zhe733 is also useful for studying the anatomical, physiological, and biochemical changes at chalkiness formation of early maturing indica rice (Shen and Cheng 1999; Jiang et al. 2002). Zhe733 and KBNT*lpa* were observed to be tolerant and susceptible to the rice water weevil (RWW) *Lissorhoptrus oryzophilus* (Kushel), respectively (J. N. Rutger personal communication). RWW is one of the most important insect pests of rice in the US (Way 2003) and Asia (Saito et al. 2005).

The KBNT*lpa*/Zhe733 RIL (KZRIL) F_{10-11} population is the first mapping population deposited at Genetic Stock–*Oryza* Collection (GSOR accession, http://www.ars.usda.gov/Main/docs.htm?docid = 8318) for distribution (Rutger and Tai 2005). A subset of this population has been used to map a gene controlling low-phytic acid (Rutger and Tai 2005; Andaya and Tai 2005). A detailed evaluation of the KZRIL population based on a set of core SSRs would enhance the ability of diverse research groups to utilize this population for mapping genes involved in yield, RB, RWW, and straighthead resistance.

The objectives of this study were: (1) to construct a SSR-based genetic linkage map; (2) to evaluate heterozygosity and degree of segregation distortion in the KZRIL population using SSR markers, and (3) to cluster these RILs according to SSR profiles.

Materials and methods

Plant materials and genomic DNA extraction and quantification

A total of 269 F_{10-11} KZRILs was used for SSR analysis. The KZRILs were planted in plastic pots to reach the 5- to 6-leaf stage in a greenhouse at 24–30°C and 14:10 h of light : dark. Rice leaves of each KZRIL (3–5 g) were harvested, rapidly frozen, and stored at -80°C. DNA extraction was performed using a procedure described by Tai and Tanksley (1990) except frozen tissues were ground with a mortar and pestle. DNA quality was estimated by running in 1% agarose-ethidium bromide (EMD Chemicals Inc., Gibbostown, NJ, USA) gels. The DNA samples from 269 KZRILs were quantified using a μQuant ^{TM} microplate spectrophotometer (Bio-Tek Instruments Inc., Winooski, VT, USA), and normalized to 5 ng/μL on a Biomek®2000 laboratory automation workstation (Fullerton, CA, USA) prior to DNA amplification.

SSR markers

The primer sequences and map position of the SSR markers were obtained from the Gramene Version 21 database (http://www.gramene.org). One hundred and sixty SSR markers were tested on both parents and 109 polymorphic markers were identified to use for this study (Fig. 1).

Marker amplification and allele determination

PCR amplification of the markers were performed in 25 μL reaction volumes consisting of 20 ng of genomic DNA, 10 mM Tris–HCl pH 8.3, 50 mM KCl, 2.5 mM $MgCl_2$, 300 nM of each primer, 1 U of Taq DNA polymerase (Promega, Madison, WI, USA). For each marker, forward primers were labeled with either 6FAM, NED or Hex (Applied Biosystems, Foster City, CA, USA or Integrated DNA Technologies, Coralville, IA, USA). The reverse primers were unlabeled to reduce the cost. DNA amplifications were performed with MJ Research Tetrad thermocyclers (Waltham, MA, USA) under the following PCR conditions: (1) initial denaturation at 94°C for 5 min; (2) 35 cycles of 94°C for 1 min, 55–67°C (marker dependent) for 1 min, 72°C for 2 min; (3) 5 min final extension at 72°C. PCR products were pooled based on color and size range of amplified fragments (typically three markers per run along with ROX-labeled size standard), and the DNA was denatured by heating samples at 94°C for 5 min. The samples were separated on an ABI Prism 3700 DNA analyzer according to the manufacturer's instructions (Applied Biosystems). The sizes of SSR fragments were determined using the software GeneScan® Version 3.7NT (Applied Biosystems) and Genotyper® Version 3.7NT (Applied Biosystems). Alleles were binned manually.

Data analysis

The genetic distance and clustering of KZRILs were determined using the software PowerMarker Version 3.23 (http://statgen.ncsu.edu/powermarker). Nei's (1972) genetic distance was used to calculate the pairwise genetic distances among all the KZRILs. Unweighted pair-group method using arithmetic average (UPGMA) was applied to cluster analysis. The cluster tree was constructed using the tree program Mega Version 3.0 (http://www.megasoftware.net). A marker locus or a KZRIL was excluded for further analyses if its successful rate of PCR amplification was lower than 75.0%. The goodness-of-fit of observed number of KBNT*lpa* and Zhe733 allele to the expected 1:1 ratio was evaluated with chi-square test by JoinMap® Version 3.0 at $P < 0.05$.

The JoinMap program was used for linkage analysis. The loci were assigned to linkage groups by the program default settings and likelihood odds ratio (LOD) scores were equal to or higher than 3.0. The map units (cM) were derived using the Kosambi function (Kosambi 1944). The order of the markers on each chromosome was referred to the SSR marker database of Cornell SSR 2001 (Cornell2001) as described in Gramene, and by Conaway-Bormans et al. (2003) and Jia et al. (2004). The ''fixed order'' command was used to identify the most probable marker order within a linkage group.

Results and discussion

Construction of a SSR linkage map

A SSR linkage map of 107 marker loci was constructed using 109 SSR markers (Fig. 1). The mapped markers covered 12 rice chromosomes in

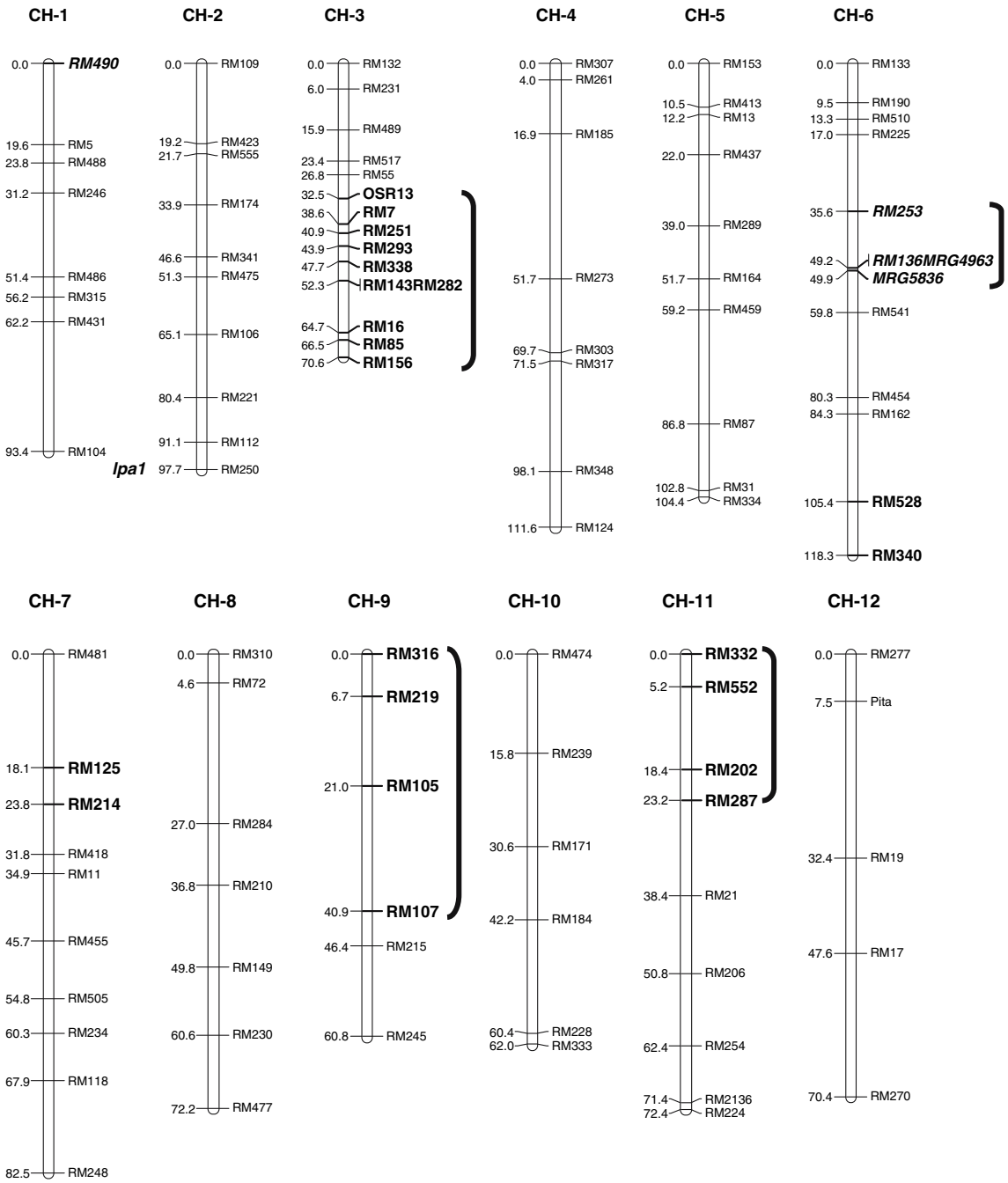

Fig. 1 A SSR map of rice showing the locations of 107 SSR markers based on 269 RILs of KBNT*lpa* × Zhe733 $F_{10–11}$ population. The genetic distances of SSR markers in cM (Kosambi function) are shown on the *left side* of each chromosome. The order of the markers is referred to the public database of Cornell SSR 2001 (Cornell2001) at Gramene (http://www.gramene.org), and the publications by Conaway-Bormans et al. (2003) and Jia et al. (2004). The Zhe733-favored markers on chromosome 3, 6, 7, 9, and 11 are indicated in *bold* and the KBNT*lpa*-favored markers on chromosome 1 and 6 in *bold* and *italic*. Segregation distortion regions are indicated by *brackets* to *right* of the linkage map. The *lpa1* locus closely linked to RM250 is indicated to the *left* of chromosome 2 on the linkage map (Anaya and Tai 2005)

1,016.3 cM of genetic distance with an average of 9.3 cM between two markers. The total genetic distance in the present population was 64.9% of that in Cornell2001 that is shorter than the genetic distance of 1,565.9 cM for the same number of the markers from Cornell2001. Only two markers RM1 (Chrom 1) and RM408 (Chrom 8) in Cornell2001 had no linkage to other markers in this population. For RM408, a gap between RM408 and RM310 with more than 50 cM may break the linkage based on their map positions in Cornell2001. In the present study, the order of the markers on chromosomes 1, 2, and 4–11 was in agreement with ones in Cornell2001. However, there were disagreements of marker order with Cornell2001 on chromosome 3 and 12. It was reported by Antonio et al. (1996) that DNA markers in five large populations of rice from different crosses were mapped at the same linkage groups with conserved linkage order, pointing out that any major genetic information from a high-density map can be expected to be approximately the same in other crosses or populations. The disagreements of the marker order in this study might be due to some closely linked markers in a relatively smaller number of the RILs in this population.

Analysis of segregation distortion

In this study, the expected segregation of a marker locus or a KZRIL fits to a ratio of 1:1 of KBNT*lpa* : Zhe733 (K/Z). Based on the predicted 1:1 segregation ratio of KBNT*lpa* to Zhe733 in KZRILs, 255 KZRILs were classified into the following groups: (1) no significant preference to either of the parents KBNT*lpa* and Zhe733 at 0.7–1.5 of the K/Z allele ratio (χ^2 = 0–3.8 and $P > 0.05$); (2) skewed in favor of KBNT*lpa* at 1.5–2.0 of K/Z allele ratio (χ^2 = 4.5–11.4 and $P < 0.05$); (3) skewed in favor of Zhe733 at 0.4–0.7 of K/Z allele ratio (χ^2 = 3.9–14.8 and $P < 0.05$); and (4) highly skewed in favor of Zhe733 at <0.4 of the K/Z allele ratio (χ^2 = 15.4–105.0 and $P < 0.01$) (Fig. 2). The majority of the KZRILs, 61.6% of the total 255 KZRILs, had no significant preference to either of the parents ($P > 0.05$). Sixty-one (23.9%) and twenty-six (10.2%) KZRILs were skewed and highly skewed toward Zhe733, respectively. Eleven KZRILs (4.3%) were skewed toward KBNT*lpa* (Fig. 2).

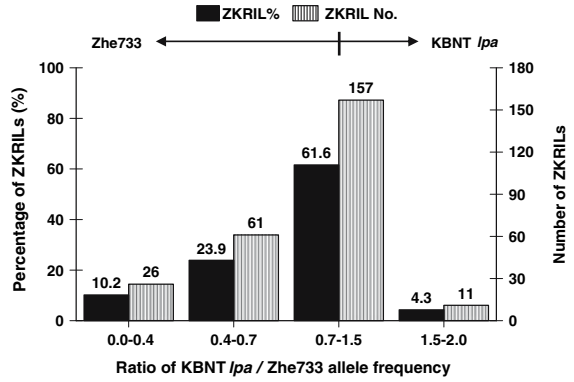

Fig. 2 Number and frequencies of skewed KZRILs by SSR markers under different categories in the ratio of KBNT*lpa*/Zhe733 allele

There were no significant preference ($P > 0.05$) to either of the parents at 55 marker loci (50.5%) (Fig. 3). However, 48 markers were found to favor Zhe733 and six markers were found to favor KANT*lpa*. Specially, 23 markers (21.1%) on chromosomes 3, 6, 7, 9, and 11 highly favored Zhe733 (χ^2 = 16.8–189.7 and $P < 0.01$) with a frequency of higher than 63.1% (Figs. 1, 3). Twenty-five (22.9%) markers favored Zhe733 (χ^2 = 4.2–15.1 and $P < 0.05$) with a frequency of 56.8–62.8% (Fig. 3). Five markers (4.6%) on chromosome 1 and 6 highly favored KBNT*lpa* (χ^2 = 18.5–46.6 and $P < 0.01$) with a frequency of 63.6–73.1%. If four or more closely linked markers on a chromosome are significantly associated with skewed segregation, this chromosomal region of skewed markers is regarded as a segregation distortion region (SDR) (Xu et al. 1997).

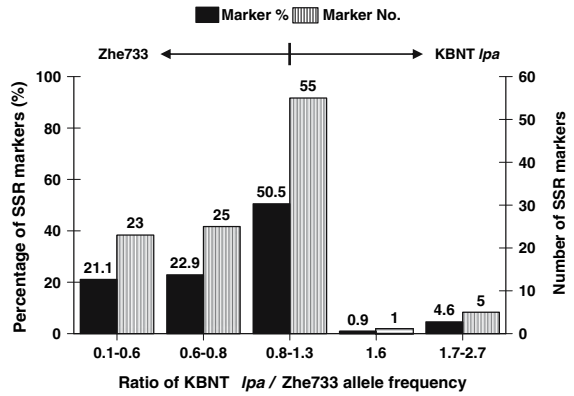

Fig. 3 Number and frequencies of skewed SSR markers that detected KBNT*lpa* and Zhe733 allele under different categories in the ratio of KBNT*lpa*/Zhe733 allele

In this study, four SDRs were found to associate with marker distortion, three SDRs skewed toward Zhe733 on chromosome 3, 9, and 11, and one SDR on chromosome 6 skewed toward KBNT*lpa* (Fig. 1). Similarly, Xu et al. (1997) reported that the SDRs on chromosome 3, 6, and 11 in a RIL rice population were located or near previously identified gametophytic gene loci (*ga*) and/or sterility loci (*S*). In an F_2 rice population, four SDRs on chromosome 3, 4, 6, and 7 were found near to *ga* or *S* genes (Zhao et al. 2006). It is possible that the segregation distortion of markers in chromosome 3, 6, and 11 in this study is likely due to the peculiar effects of *ga* or *S* genes. Distorted segregation of molecular markers has been previously observed in mapping populations derived from intra- and inter-specific hybrids in many crops including wheat (Peng et al. 2000), potato (Gebhardt et al. 1989), corn (Gardiner et al. 1993), and barley (Heun et al. 1991). Xu et al. (1997) also reported that significantly higher frequencies of distorted markers were observed in RIL populations than other populations of F_2, backcrossing and doubled haploid. In contrast with our study, it was found that other *japonica*/*indica* RIL population previously had significantly more distorted markers (Wang et al. 1994; He et al. 2001; Andaya and Mackill 2003).

The causes of segregation distortion can be a number of physiological or genetic factors such as gametic or zygotic selection (Nakagahra 1986; Peng et al. 2000), chromosome rearrangement (Tanksley 1984), genetical incompatibility (Cryder et al. 1991; Liedl and Anderson 1993), pollen competition (Mangelsdorf and Jones 1926; Liedl and Anderson 1993), and preferential fertilization (Schwemmle 1968; Gadish and Zamir 1986). It is generally believed that differential gametophytic selection was responsible for segregation distortion in rice (Xu et al. 1997; He et al. 2001; Zhao et al. 2006) and in maize (Lu et al. 2002).

Heterozygosity and non-parental alleles

Theoretically, the average frequencies of heterozygous loci in a F_{10} and F_{11} RIL population should be 0.2 and 0.1%, respectively. In this study, the frequencies of heterozygous KZRILs were 0–3.7% with an average of 1.3%. The average frequency of overall heterozygosity per KZRIL was 1.3% ranging from 0 to 38.9%. The average frequency of overall heterozygosity per RILs was 3.6% in the F_7 RIL population of 9024 (*indica*) and LH422 (*japonica*) (Xiao et al. 1996) and in the F_{11} RIL population from the cross between Milyang 23 (*indica*/*japonica*) and Gihobyeo (*japonica*) (Cho et al. 1998). Even though the frequency of heterozygous loci in our study (1.3%) is slightly higher than the theoretical values, it is still obviously lower than the average frequencies reported by Xiao et al. (1996) and Cho et al. (1998). Of 109 markers tested across 255 KZRILs, ten markers loci (9.2%) were homozygous, 53 markers loci (48.6%) were heterozygous in up to nine KZRILs/markers, ten markers loci (9.2%) had non-parental alleles in up to seven KZRILs/markers, 36 markers loci (33.0%) had both heterozygous and non-parental alleles. Of 255 KZRILs detected across 109 markers, 172 KZRILs (67.5%) were homozygous; 42 KZRILs (16.4%) were heterozygous at a highest marker locus of 42. The KZRILs of GSOR346, GSOR73, and GSOR184 were heterozygous at 42, 39, and 34 markers loci in as high as 38.9, 36.8, and 32.1%, respectively (Table 1).

The occurrence of non-parental alleles is much less common than heterozygosity. The non-parental alleles in KZRILs were probably caused by pollen contamination in advancing KZRIL since the panicles of KZRILs were not bagged at rice flowering stage. It could also be due to low abundance parent alleles that become predominant in the progeny. The frequencies of non-parental alleles were 0–3.7% with an average of 0.4%. Thirty KZRILs (11.8%) had up to nine non-parental alleles, and 11 KZRILs (4.3%) were heterozygous with non-parental alleles. The average frequency of overall non-parental alleles per KZRIL was 0.4% ranging from 0 to 15.0%.

A KZRIL with more than five heterozygous marker loci or non-parental alleles was defined as a heterozygous KZRIL or a non-parental KZRIL in this study. Thirteen heterozygous KZRILs and nine non-parental KZRILs were found representing 5.1 and 3.5% of the total 255 KZRIL population. Together, 20 heterozygous KZRILs and KZRILs with non-parental alleles were excluded from cluster analysis (Table 1).

Clustering of KZRILs

Cluster analysis of RILs would allow the selection of representative lines for the traits, which are difficult

Table 1 List of KBNT*lpa* × Zhe733 RILs (KZRILs) heterozygote at more than five marker loci and KZRILs with more than five non-parental alleles and their percentages

KZRIL accession	Heterozygosity		KZRIL accession	Non-parental allele	
	Marker locus	%		Marker locus	%
GSOR346	42	38.9	GSOR5	12	15.0
GSOR73	39	36.8	GSOR35	10	12.3
GSOR184	34	32.1	GSOR301	9	9.7
GSOR266	29	28.7	GSOR338	9	9.0
GSOR347	25	26.6	GSOR307	8	8.7
GSOR55	21	20.4	GSOR321	6	6.1
GSOR350	21	19.4	GSOR53	6	5.8
GSOR48	18	16.7	GSOR285	5	5.1
GSOR203	16	14.8	GSOR197	5	4.8
GSOR264	13	13.7			
GSOR84	11	10.2			
GSOR35	8	10.1			
GSOR307	8	8.7			

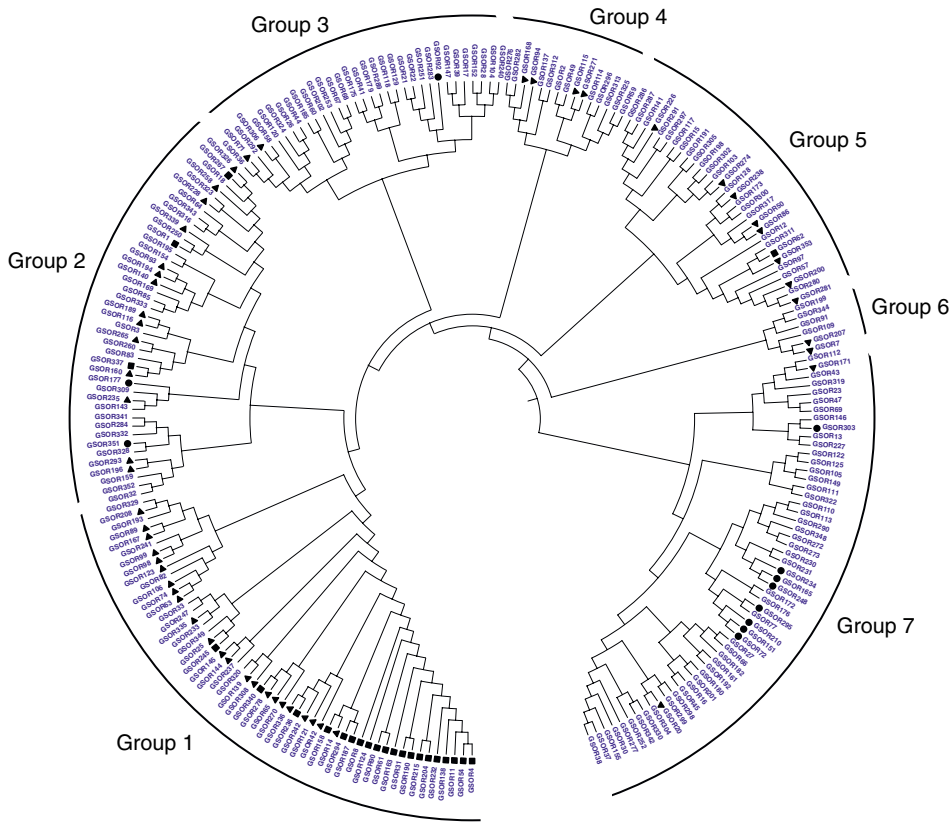

Fig. 4 Clustering of 235 KZRILs. KZRILs (GSOR accessions) are clustered into seven groups using UPGMA method based on Nei's (1972) genetic distance. The KZRILs indicated with the symbols of *filled square*, *filled diamond*, and *filled circle* are highly skewed toward Zhe733 ($\chi^2 > 15.4$, $P < 0.05$), skewed toward Zhe733 ($\chi^2 = 3.9$–14.8 and $P < 0.05$) and toward KBNT*lpa* ($\chi^2 = 4.5$–11.4 and $P < 0.05$), respectively

to phenotype, for example, RWW resistance. Accurate responses of rice plants to RWW is difficult to determine because RWW cannot be massively reared in an environment-controlled condition (Zhang et al. 2004) and field evaluation of RWW resistance is only feasible with a small number of test entries (Stout and Riggio 2002). Therefore, clustering of KZRILs will be particularly beneficial for the selection of representative RILs based on the genetic variation. Cluster analysis was applied to 235 KZRILs using UPGMA method based on Nei's (1972) genetic distance. The dendrogram obtained showed a clear separation of the KZRILs and seven groups of KZRILs were divided (Fig. 4). The KZRILs highly skewed toward Zhe733 (χ^2 = 15.4–105.0 and $P < 0.05$) were mainly in Group 1. Other KZRILs skewed in favor of Zhe733 (χ^2 = 3.9–14.8 and $P < 0.05$) were mainly in Group 1, 2, and 5 and the KZRILs skewed in favor of KBNT*lpa* (χ^2 = 4.5–11.4 and $P < 0.05$) were mainly in Group 7.

In conclusion, the KBNT*lpa* × Zhe733 RIL F_{10-11} population is a good mapping population characterized by relatively low frequencies of heterozygosity and non-parental alleles, and by relatively low percentages of skewed markers and skewed KZRILs. This SSR marker information and the linkage map would be valuable for cloning the critical genes for yield, RB, RWW, and straighthead resistance.

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